

A survey of valvae of *Euphydryas chalcedona*, *E. c. colon*, and *E. c. anicia*

James A. Scott

60 Estes Street, Lakewood, Colorado 80226

Abstract.—A survey of male valvae of almost 500 *Euphydryas chalcedona*, *E. c. colon*, and *E. c. anicia* in western North America demonstrates that very many populations are intermediate between these entities. Six intergrading valval types are recognized, and populations exist having each of these types as the mode. Male valvae therefore do not support treating these three as distinct species. Because wing pattern shows complex patterns, with many intermediate populations, these three entities should be treated as subspecies of *chalcedona*.

Introduction

Before 1927 the *Euphydryas* of North America, except for *E. phaeton* (Drury) and *gillettii* (Barnes) were in chaos with about 30 "species." Then McDunnough (1927) and Gunder (1929) used male genitalia to reduce the number of species to five. They include in *E. editha* (Boisduval) populations with a distinctive valva and reduced uncus with two short blunt projections. They treated *chalcedona* (Doubleday), *colon* (Edwards), and *anicia* (Doubleday) as two species, *chalcedona* (with *colon*) and *anicia*, which all have a bifid uncus with two curved claw-like hooks. *E. chalcedona* and *colon* were found to have the same short dorsal valval process, whereas *anicia* was found to have a longer process. Their treatment has been followed more or less unchanged until now, although Bauer (1975) treats *colon* as a distinct species.

I recently collected populations with male valvae intermediate between *chalcedona-colon* and *anicia*. This paper is a detailed survey of male valvae, concentrating on areas where intermediates in valvae or wing pattern occur. It proves the existence of numerous populations over a large area that are intermediate in valvae. This, together with other published evidence, leads me to conclude that *colon* and *anicia* both belong to the highly polytypic polymorphic species *chalcedona*.

Methods

Males of each population were examined and tabulated in Table 1 according to best resemblance to the drawings in Fig. 1. The dorsal wing pattern was rated in Table 1 according to whether the overall appearance is blackish, whitish, or reddish. There are numerous other

wing characters involved (Hovanitz & Le Gare 1951) which this paper does not consider.

Results and Discussion

The samples fall into three arbitrary categories: *chalcedona-colon* (mostly a or b of Fig. 1), *ancia* (mostly e or f), and intermediates between the two (c or d). Some samples have a the usual form, others have b, c, d, e, or f (Table 1). There are clearly many intermediate populations. These occur almost everywhere between the ranges of *chalcedona-colon* and *ancia*, including California, Arizona, Nevada, Washington and Montana. They are probably found in Idaho, Oregon, and British Columbia also (intermediate populations are reported for the Wallowa Mts. Oregon.) McDunnough's *paradoxa* from B.C. has somewhat intermediate genitalia (McDunnough 1927). In wing pattern the *chalcedona* and *colon* samples are very similar, black with cream spots. The *ancia* samples are usually some shade of reddish or cream-colored, rarely blackish. The intermediate genitalia samples have every type of wing pattern, and many of the populations are polymorphic in wing pattern, as are some of the *ancia* samples. The large number of samples intermediate in valvae proves conclusively that valvae cannot be used as the basis for dividing the populations into separate species.

Turner et al. (1961) show that genitalia differences do not necessarily indicate separate species are involved. They showed that the phenotype of *Papilio dardanus* Brown with a long process on the valva is due to a dominant gene, whereas the phenotype with a short process is due to its homozygous recessive allele.

A character mentioned by Bauer (1961), the minute spines on the upper process, is not useful. All samples have the dorso-posterior rim of the upper process with minute teeth. The teeth are dense on short processes and less dense on longer processes as if the same number of teeth are spread over a larger area. Associated with a long upper process is a slightly longer lower process having a reduced anterior bump. This bump sometimes is formed into a separate lobe making a bifurcate lower process, frequent in ssp. *quino* (Behr).

Gradual clinal changes in the proportions of valval forms seem to occur in some geographic areas, whereas more abrupt changes seem to occur in other areas. This is also true of the wing pattern, which is almost hopelessly complex, making the use of subspecies very dubious. Jewett (1959) accordingly suggested that further naming of subspecies be stopped.

The most reasonable interpretation of the genitalic intermediates is that of only one polytypic polymorphic species, *chalcona*. The name *chalcona* has page priority over *anicia*, being named on Fig. 1 versus Fig. 2 for *anicia* in the same paper.

Bauer (1975) states that in several places *colon* is sympatric with *chalcona* and *anicia*, although these places are not stated or the statements documented. However, I cannot distinguish genitalia of *chalcona* from *colon* and suspect that apparent cases of sympatry really are polymorphisms. Certainly such cases, if they exist, should be fully investigated and the results published. Populations only a few hundred meters from each other may exchange very few individuals and fluctuate in population size independently (Ehrlich et al. 1975), so the occurrence of two forms in the same region does not necessarily prove that they are distinct species.

The larval web character of *colon* cited by Bauer (1975) is not diagnostic because *chalcona* and *anicia* also have webs. *E. c. capella* (Barnes) webs its *Penstemon* hostplant so extensively that defoliated plants look as if a nylon stocking had been placed over them. Dammers (1940) and Bauer (1975) state that *colon* has whiter larvae than *chalcona* although Bauer states that *colon* has less white on the body than some other populations.

The one-species interpretation has also been suggested by previous work. Lionel Higgins (pers. comm.), in an unpublished study done many years ago, was not able to define the species to his satisfaction using genitalic characters. McDunnough (1927) showed that his "*colon*" *paradoxa* McDunnough has a longer dorsal valval process than does "*colon*" *perdiccas* (Edwards) and has redder wings, both traits tending toward *anicia*; wing pattern of *paradoxa*, and of *anicia* from Keremeos B. C., is identical. The original description of *wallacensis* Gunder (Gunder 1928a), previously placed in *colon* by Bauer (1975), states "genitalia of this race approach the *anicia* group" and "this race probably represents a connecting link as Dr. McDunnough has suggested." The holotype of *irelandi* Gunder has intermediate genitalia and was placed in *anicia* by Gunder (1929) and dos Passos (1964), in *chalcona* by Bauer (1975). Gunder (1928b) described red versus white or black forms connected by intergrades for two populations [*mcglashanii* (Rivers) black, *truckeensis* Gunder red; *olancha* (Wright) whitish, *georgei* Gunder red]. The genitalia figure of *georgei* by Gunder (1929) is intermediate. Dammers (1940) successfully hybridized and backcrossed *chalcona* and *kingstonensis* Emmel and Emmel which are very different in appearance. *E. c. hermosa* (Wright)

was placed in *anicia* by Gunder (1929) and Bauer (1975), but in *chalcedona* by dos Passos (1964) and Emmel and Emmel (1972); *kingstonensis*, *klotsi* dos Passos, *hermosa*, and *morandi* Gunder all have very similar wing pattern, yet have been placed in several "species." Bauer's (1975) subspecies of "*colon*" from Elko Co. Nevada is stated to have white, red, and black forms. Red populations from California (*sierra* [Wright]) and Arizona (*klotsi*) have been included among the west coast black populations in the same species *chalcedona* by Gunder (1929), dos Passos (1964), and Bauer (1975). Finally, dos Passos (1964), McDunnough (1927), and Gunder (1929) treated *colon* and *chalcedona* as conspecific.

In many places in the intergradation zone in western U.S. the male valvae change from one form to another at a different place than the wing pattern. Wing patterns change in regions where valvae do not (many places), and valvae change in regions where wing patterns do not (such as in British Columbia, Arizona, and Nevada). This phenomenon of non-concordance of characters is typical of many polytypic species, such as for wing characters of *Speyeria callippe* (Boisduval) (Hovanitz 1943). When separate species are involved most characters usually change at the same place.

Higgins (1978) has split the genus *Euphydryas* into four separate genera, placing *editha*, *chalcedona*, *c. colon*, and *c. anicia* into *Occidryas* Higgins; I prefer to treat these names as subgenera to avoid the awful fate of the birds, in which each species is in its own genus.

Acknowledgements: I thank Ernst J. Dornfeld, Robert E. Woodley, Steven J. Kohler for providing specimens and reading the manuscript, and Stanley G. Jewett Jr. and Paul R. Ehrlich for reading the manuscript.

Literature Cited

- BAUER, D. L. 1961. In: P. R. and A. H. Ehrlich, How to know the butterflies. Wm. Brown Co., Dubuque, Iowa.
- BAUER, D. L. 1975. In: W. Howe, ed. The butterflies of North America. Doubleday and Co. Inc. N.Y.
- DAMMERS, C. M. 1940. *Euphydryas chalcedona*. Bull. So. Cal. Acad. Sci. 39:123-125.
- DOS PASSOS, C. F. 1964. A synonymic list of the nearctic rhopalocera. The Lepid. Soc. Mem. #1.
- EHRLICH, P. R., R. R. WHITE, M. C. SINGER, S. W. McKECHNIE, L. E. GILBERT. 1975. Checkerspot butterflies: a historical perspective. Science 188:221-228.
- EMMEL, T. C., & J. F. EMMEL. 1972. Two new subspecies of *Euphydryas chalcedona* from the Mojave desert of southern California. J. Res. Lepid. 11:141-146.

- GUNDER, J. D. 1928a. New *Euphydryas*. Pan-Pacific Ent. 5:49-50.
- GUNDER, J. D. 1928b. New Butterflies. Entom. News 39:304-306.
- GUNDER, J. D. 1929. The genus *Euphydryas* of boreal america. Pan-Pacific Ent. 6:1-8.
- HIGGINS, L. G. 1978. A revision of the genus *Euphydryas* Scudder (Lepidoptera, Nymphalidae). Entom. Gazette 29:109-115.
- HOVANITZ, W. 1943. Geographical variation and racial structure of *Argynnis callippe* in California. Amer. Natur. 77:400-425.
- HOVANITZ, W., & M. J. Le GARE. 1951. Genetic and ecologic analyses of wild populations in lepidoptera. II. Color pattern variation in *Melitaea chalcadon*. Wasmann. J. Biol. 9:257-310.
- JEWETT, S. G., Jr. 1959. Concerning subspeciation in western North American *Euphydryas*. J. Lepid. Soc. 13:171-173.
- MCDUNNOUGH, J. 1927. The lepidoptera of the Seton Lake region, British Columbia. Can. Ent. 59:152-162.
- TURNER, J. R. G., C. A. CLARKE, & P. M. SHEPPARD. 1961. Genetics of a difference in the male genitalia of east and west African stocks of *Papilio dardanus*. Nature 191:935-936.

TABLE I

Number of individuals of each valval type (a to f of Fig. 1), and predominant wing color and subspecies, for each locality.

Locality	a	b	c	d	e	f	Main Color	Subspecies
Jerseydale, Mariposa Co. Calif.	-	-	1	-	-	-	black, cream	chalcadon
Indian Flat, Mariposa Co. Cal.	-	2	-	-	-	-	black, cream	chalcadon
El Portal, Mariposa Co. Cal.	1	-	-	-	-	-	black, cream	chalcadon
Lang Crossing, Nevada Co. Ca.	2	1	-	-	-	-	black, cream, red	chalcadon
Foote Crossing, Sierra Co. Ca.	1	2	-	-	-	-	black, cream	chalcadon
Blue Ravine, Sierra Co. Ca.	-	-	1	-	-	-	black, cream, red	chalcadon
Fiddle Crk., Sierra Co. Ca.	-	1	1	-	-	-	black, cream	chalcadon
Whiskeytown Res., Shasta Co. Calif.	5	4	1	-	-	-	black, cream	chalcadon?
Cedar Pass, Modoc Co. Ca.	-	1	-	-	-	-	black	colon
SE Copper, Siskiyou Co. Ca.	3	4	1	1	-	-	black, cream	colon?
Kinney Crk., Jackson Co. Ore.	-	2	-	-	-	-	black, cream	colon?
French Gulch, Jackson Co. Ore.	1	1	-	-	-	-	black, cream	colon?
Illinois R. rd., Josephine Co. Ore.	-	1	-	-	-	-	black, cream	colon?
Wolf Creek, Josephine Co. Ore.	1	2	-	-	-	-	black, cream	colon?
Bly Mtn., Klamath Co. Ore.	4	4	1	-	-	-	black, cream, red	colon-dwinellei Hy. Edw.
S. La Pine, Klamath Co. Ore.	1	-	-	-	-	-	black, cream	colon-dwinellei
Odell L., Klamath Co. Ore.	2	1	-	-	-	-	black, cream	colon?
Hart L., Linn Co. Ore.	1	-	-	-	-	-	black, cream	colon
Monument Pk, rd. Linn Co. Ore.	1	1	-	-	-	-	back, cream	colon

Cascadia, Linn Co. Ore.	1	-	-	-	-	black, cream	colon
Cascadia S. Park, Linn Co. Ore.	1	-	-	-	-	black, cream	colon
nr. Halfway, Baker Co. Ore.	-	3	1	-	-	black, cream	wallacensis
Lost Prairie, Linn Co. Ore.	-	1	-	-	-	black, cream	colon
SE Drew, Douglas Co. Ore.	-	1	-	-	-	black, cream	colon
McDonald Forest, Benton Co. Ore.	1	-	-	-	-	black, cream	colon

Locality	a	b	c	d	e	f	Main Color	Subspecies
Siskiyou Summit, Jackson Co. Ore.	2	1	-	-	-	-	black, cream	colon
Satus Pass, Yakima Co. Wash.	-	1	-	-	-	-	black, cream, some red	paradoxa?
Hurricane Ridge Clallam Co. Wash.	8	3	-	-	-	-	black, cream	perdiccas
Tucannon R., Columbia Co. Wash.	1	-	-	-	-	-	black, cream	wallacensis
Horse Crk., Wallowa Co. Ore.	1	-	-	-	-	-	black, cream	wallacensis
Camas Prairie, Sanders Co. Mont.	-	2	-	-	-	-	black, cream, some red	wallacensis
Gilbreth Spgs., Columbia Co. Wash.	-	-	1	-	-	-	black, cream	wallacensis
9-mile Crk., Missoula Co. Mont.	-	-	2	-	-	-	black, cream	wallacensis
Pattee Can., Missoula Co. Mont.	-	-	2	4	-	-	black, cream	wallacensis
Miller Crk., Missoula Co. Mont.	-	1	10	17	8	-	black, cream	wallacensis
Warm Spgs. Cgd., Ravalli Co. Mont.	-	-	-	1	-	-	black, cream, red	howlandi S. & T.?
Ronan, Lake Co. Mont.	-	-	-	1	-	-	cream, black	bernadetta?
SE Easton, Yakima Co. Wash.	-	1	1	2	-	-	some black, some red-cream	hopfingeri Gunder?
Peoh Peak, Kittitas Co. Wash.	1	1	-	4	-	-	black, cream	paradoxa?
Rush Creek, Washoe Co. Nev.	-	-	-	12	8	1	cream, black, some red	veazieae F. & J.
N. Hallelujah Jct. Lassen Co. Cal.	2	5	3	1	1	-	black, cream, some red	veazieae-sierra?
Bartle, Siskiyou Co. Cal.	-	2	2	-	-	-	black, forewing reddish	dwinellei
Kin Can., Ormsby Co. Nev.	-	4	3	1	-	-	cream, black, sl. red	olancha-sierra?
Loon Lake, El Dorado Co. Ca.	-	14	8	3	-	-	red to black, sl. cream	sierra
Sonora Pass, Tuolumne Co. Calif.	-	-	-	1	2	2	black-cream-red	sierra-olancha
Ebbets Pass, Alpine Co. Ca.	-	-	-	1	-	-	red	sierra
Hermit Valley, Alpine Co. Calif.	-	-	1	-	-	-	red	sierra
Echo Lake, El Dorado Co. Ca.	1	2	1	2	-	-	red	sierra

Carson Pass, Alpine Co. Ca.	9 16 19 5 1 -	red to black, mixed	sierra?
Big Pine Mdw., Tulare Co. Calif.	3 9 3 - - -	cream, some red-black	olancha?
Oak Crk. Can., Coconino Co. Ariz.	- 1 2 5 - -	ochre, some black- cream	klotsi
N. Canyon, Yavapai Co. Ariz.	- - 3 - - -	ochre, some black- cream	klotsi
Yava, Yavapai Co. Ariz.	- - 2 - - -	ochre, some black- cream	klotsi

Locality	a b c d e f	Main Color	Subspecies
Providence Mts. San Bern. Co. Calif.	- 2 10 1 - -	ochre	kingstonensis
Rock Corral, San Bern. Co. Calif.	1 1 2 - - -	red	corralensis E. & E.
E. Jacumba, San Diego, Co. Ca.	- 1 3 1 - -	cream, black	quino
W. Jacumba, San Diego Co. Ca.	- 2 2 - - -	cream, black	quino
E. Jacob Lake, Coconino Co. Ariz.	- - - - 1 1	ochre	hermosa?
Peppersauce Can., Pima Co. Ariz.	- - - - 2 1	ochre	hermosa
Horseshoe Cienega, Apache Co. Ariz.	- - - - 2 3	ochre-red-black cream	magdalena B. & McD.
Mt. Wheeler Scenic Area, White Pine Co. Nev.	- - - - 2	red, cream	wheeleri
Austin Summit, Lander Co. Nev.	- - - - 1	red, cream	wheeleri
W. Durkee, Baker Co. Ore.	- - - - 2 -	white, some red	bakeri S. & T.
Trout Crk. Rd., Harney Co. Ore.	- - - - 1 1	white, some red	macyi F. & J.
Wildhorse Crk., Harney Co. Ore.	- - - - 1	white, some red	macyi
Salmon Mdws., Okanogan Co. Wash.	- - - - 2 2	black, red, cream	hopfingeri
Humphrey, Clark Co. Idaho	- - - - 1	black, red, cream	howlandi?
Swan L., Madison Co. Mont.	- - - - 3	black, red, cream	howlandi?
S. Norris, Madison Co. Mont.	- - - - 2 5	cream, black	bernadetta Leussler
4 Mile Crk., Sweet Grass Co. Mont.	- - - - 1 -	red, some black- cream	windi Gunder?
5 mi. S. Wasa, B.C.	- - - - 1 1	red, some black- cream	ancia
Ft. Steele, S. Wasa, B.C.	- - - - 2	red, some black- cream	ancia
Elko, B.C.	- - - - 2 3	red, some black- cream	ancia
8 mi. W. Cranbrook B.C.	- - - - 1	red, some black- cream	ancia
Halfmoon Park, Sweet Grass Co. Mont.	- - - - 1	cream, black	bernadetta

Swamp Crk., Sweet Grass Co. Mont.	- - - - 1	cream, black	bernadetta
McLeod, Sweet Grass Co. Mont.	- - - - 3 5	cream, black, red	howlandi?
Polaris, Beaverhead Co. Mont.	- - - - 5 5	cream, black, red	howlandi
Bozeman, Gallatin Co. Mont.	- - - 1 2 4	cream, black, red	howlandi
Gallatin Mts., Gallatin Co. Mont.	- - - - 1 6	cream, black, red	bernadetta- howlandi
Bridger Can., Carbon Co. Mont.	- - - - 1 1	cream, black, red	same
Mile 154, Haines Jct., Yukon	- - - - 3 1	red, black, cream	helvia Scudder

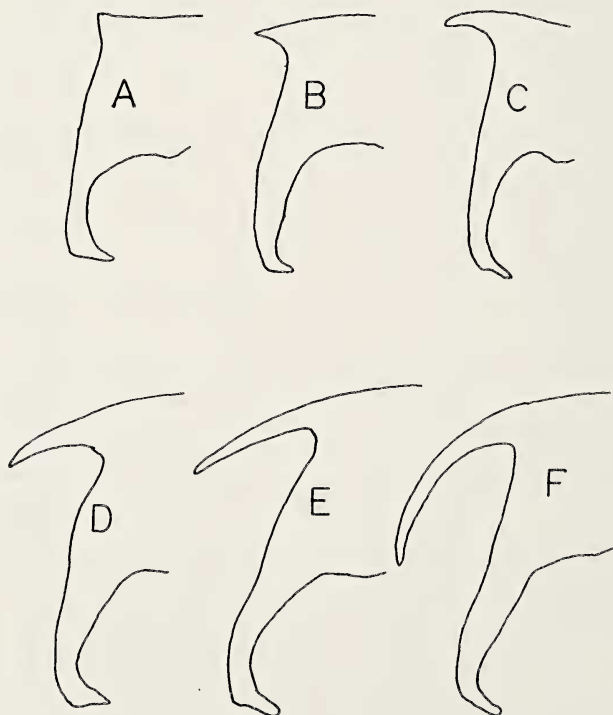


Figure 1. Six shapes of the valval process in *Euphydryas chalcedona*, *E. c. colon*, and *E. c. anicia* used in Table I.